

LIFE HISTORY OF *NEOTEPHRTIS FINALIS* (LOEW) ON
NATIVE ASTERACEAE IN SOUTHERN CALIFORNIA
(DIPTERA: TEPHRITIDAE)

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Abstract.—*Neotephritis inornata* (Coquillett) is synonymized with *N. finalis* largely based on examination of reared specimens. New host-plant records for *N. finalis* are presented, and selected published records confirmed or questioned. An affinity for hosts in the subtribe Verbesininae of the tribe Heliantheae (Asteraceae) is noted. The biology of this multivoltine tephritid in flower heads of *Encelia farinosa* Gray is described, one of a succession of host-plant species in which it reproduces throughout the year in various parts of southern California. The primary, hymenopterous, solitary, larval or larval-pupal parasites, *Eurytoma vernonia* Bugbee (Eurytomidae) and *Pteromalus* sp. (Pteromalidae) are reported from *N. finalis*.

Neotephritis finalis (Loew) commonly infests the flower heads of many Asteraceae in southern California. Herein we record our collective findings on this heretofore little-known fly studied irregularly by us since 1980.

TAXONOMY

Foote (1960) reviewed the three species of *Neotephritis* known from North America. Only *N. finalis* and *Neotephritis inornata* (Coquillett) are known from California (Foote and Blanc, 1963), the latter species only from two solitary, swept or trapped male specimens. Swept and reared specimens of *Neotephritis* collected by RDG in California appeared to vary in the key characters that have been used to separate *inornata* and *finalis*. This prompted a detailed examination of specimens of *Neotephritis* reared from extensive samplings of mature flower heads of native Asteraceae from central and southern California to determine if the two species are distinct.

The key provided by Foote and Blanc

(1963) separated *finalis* from *inornata* by two characters: specimens with two light spots in cell r_{4+5} immediately anterior of vein M and the ovipositor sheath darkened apically were considered *finalis*; specimens with three small hyaline spots in r_{4+5} and a basally darkened ovipositor sheath were called *inornata*. Steyskal (1972) provided a key to 11 species of *Neotephritis* in which he separated *finalis* from *inornata* by two additional characters: in *finalis*, cell dm (discal cell) with a distinct hyaline spot close to its postero-apical corner and the scutellum largely rufous medially; in *inornata*, cell dm without a distinct hyaline spot close to its postero-apical corner and the scutellum rufous along its hind margin.

Two hundred and forty-five mounted specimens of *Neotephritis* reared from five genera and 12 species of Asteraceae from 24 different locations during 1980-86 by RDG were examined. All of these specimens would key to either *finalis* or *inornata* in Steyskal (1972) and Foote (1960). These specimens, which were largely randomly se-

lected and mounted, comprised 126 (51.4%) ♂ and 119 (48.6%) ♀ and represented subsamples from more than twice this number of reared flies. Among the males examined, there were 12 (9.5%) from eight locations that lacked an apical spot in the postero-apical corner of cell dm on both wings, 7 (5.6%) that lacked a spot on one wing, but with a faint or small spot, or in two instances, a prominent spot on the other wing, and eighty (63.5%) ♂ with a large spot on both wings, and 27 (21.4%) with a large spot on one wing and a tiny or faint spot on the other. Similarly, among females, 9 (7.6%) from seven locations lacked the spot on both wings, and 4 (3.4%) lacked a spot on one wing, but possessed a faint, small, or, in one case, a prominent spot on the other. Eighty-seven (73.1%) ♂ had prominent spots in both wings, and 19 (16.0%) showed greatly reduced or faint spots in one or both wings. Clearly, this wing character used by Steyskal (1972) varies too continuously among both sexes of specimens from southern California to segregate them into different species.

None of the above 245 reared specimens examined had a partially or wholly rufous scutellum. Instead, both sexes possessed a yellowish-white central longitudinal stripe on the scutellum that varied in length from a narrow posterior band to a prominent apical spot to nearly bisecting this segment, and was bounded by dark lateral stripes and an overlay of dark to light grey microtomentum. Examination of the male syntype by A. L. Norrbom (*in litt.* 1987) as well as one of the two female syntypes of *inornata* from the type locality, i.e. Las Vegas Hot Springs, New Mexico, on loan to RDG from the National Museum of Natural History (USNM) collection, confirmed that the scutellum of both was rufous brown with the lateral and posterior third yellowish. Rufous or not, scutellum markings varied too much among reared specimens in southern California to use this character to segregate them.

Similarly, ovipositor sheath color was examined in 102 of the females reared by RDG

that did not have this structure discolored by dried feces or obscured by overlapped wings. In all but 2 (2.0%) ♀, a dark apical band was present, which varied from narrow to broad. More importantly, 75 (73.5%) showed at least some basal darkening of the ovipositor sheath. Only a single specimen had a unicolored, undarkened, rufous-yellow ovipositor sheath. Obviously, this character also showed too much continuous variation in reared specimens to support its use in distinguishing *inornata*.

This leaves the key character mentioned by Coquillett (1902), and used by Foote (1960), Foote and Blanc (1963), and Steyskal (1972) to separate *inornata* from *finalis*, i.e. three versus two spots in cell r_{4+5} immediately anterior of vein M. Eight (0.5%) of 201 ♂ reared by RDG during 1980–86 had the three spots diagnostic of *inornata* on one wing; 2 (0.1%) had the three spots on both wings (in one case, four spots on one wing). Similarly, 7 (3.7%) of 190 ♀ had the three spots on one wing; 1 (0.5%) ♀, the three spots on both wings. Possession of these spots was the one basis for retaining, mounting, and separately storing specimens reared during this period. These specimens varied in the ovipositor sheath and scutellum characters described above similar to specimens with only two spots in r_{4+5} in both wings. No correlation in any of three characters was detected. The specimens with three spots were reared from four genera and seven species of Asteraceae, and from eight widely separated locations in southern California along with specimens with two spots in all cases. The central or proximal spots usually were the smaller of the three, but all three spots were equally large in one wing of three specimens, 2 ♂ and 1 ♀, and on both wings of 1 ♀. Had this latter female been trapped or swept, like all reported specimens of *inornata*, not reared among a large series of specimens with only two spots in r_{4+5} , it, too, would probably have been identified as *inornata*. Comparison of this individual with three specimens of *inornata*

on loan from the USNM, each identified by different tephritid taxonomists, showed no obvious distinctions unaddressed above. Short series of specimens from the same locations in Arizona, Oregon, and Utah selected from the USNM collection by A. L. Norrbom and loaned to RDG also showed variation in the number of spots in cell r_{4+5} and other characters addressed above, which demonstrated that this variation was not confined to southern California. Therefore, the senior author (RDG), independent of his coauthors, recommends that *N. inornata* (Coquillett, 1902) be synonymized with *N. finalis* (Loew, 1862), because the name is based on a character, which is rare but continuously variable among specimens that otherwise appear conspecific.

DISTRIBUTION AND HOST PLANTS

Foote (1960, p. 149) termed *N. finalis* "one of the most commonly encountered tephritids in North America." Foote and Blanc (1963, p. 35) described its geographic range as "Southern Canada; northern Mexico; the Continental United States except Alaska and New England." *N. finalis* is widely distributed throughout California (Foote and Blanc, 1963, Map 35), including coastal central California and the Mojave Desert, areas unmarked by collection points on its state distribution map in Foote and Blanc (1963) (Goeden, unpublished data).

New host-plant genus or species records determined by comparison with Wasbauer (1972) are reported for *N. finalis* from southern California. These represent rearings from samples of mature flower heads collected and processed by RDG, as described elsewhere (Goeden, 1985). Host-plant records that are not reported in Wasbauer (1972) are labeled with a double or single asterisk for genera and species, respectively. Among multiple samples of a particular plant species, only the sample from which the most individuals was recovered is reported. The plant nomenclature

used follows Munz (1974). Rearing records are listed alphabetically.

Balsamorhiza deltoidea* Nuttall, 16 ♂ and 9 ♀, Burnt Peak, Angeles Nat. Forest, NW Los Angeles Co., 8 vi 1983; **Encelia frutescens* Gray, 8 ♂ and 6 ♀, Zzyxx offramp on Interstate Hwy. I-15, SW of Baker, San Bernardino Co., 29 iv 1981; **Encelia virginensis* A. Nelson, 8 ♂ and 2 ♀, Bautista Canyon, Riverside Co., 29 iv 1980; *Geraea canescens* Torrey and Gray, 41 ♂ and 32 ♀, Hidden Springs (NW of Indio), Riverside Co., 14 iv 1981; **Helianthus gracilentus* Gray, 2 ♂ and 2 ♀, Moreno, Riverside Co., 19 v 1981; **H. niveus* (Benth) Brandegees ssp. *tephrodes* (Gray) Heiser, 34 ♂ and 40 ♀, sand hills near Glamis, Imperial Co., 28 i 1982; ***Viguiera deltoidea* Gray var. *parishii* (Greene) Vasey and Rose, 1 ♀, Chino Canyon, Riverside Co., 3 iv 1980; **Wyethia ovata* Torrey and Gray, 2 ♂ and 3 ♀, Filaree Flat, Laguna Mountain, Cleveland Nat. Forest, San Diego Co., 14 vi 1984.

In addition, the following rearing records confirmed host records for *N. finalis* in Wasbauer (1972): *Encelia californica* Nuttall, 17 ♂ and 13 ♀, Seacliff, Ventura Co., 1 iv 1981; *Encelia farinosa* Gray, 18 ♂ and 12 ♀, above Parker Dam, SE San Bernardino Co., 30 iii 1984; *Helianthus annuus* L., 1 ♂ and 2 ♀, Canebrake, Kern Co., 8 ix 1986; *Wyethia mollis* Gray, 14 ♂ and 13 ♀, Bald Eagle Peak, Piute Mountain, Sequoia Nat. Forest, NE Kern Co., 2 vii 1982.

Additional hosts of *N. finalis* reportedly include *Aster spinosus* Benth, *Balsamorhiza sagittata* (Pursh) Nuttall, *Dahlia* sp., *Eriophyllum lanatum* (Pursh) Forbes, *Gailardia aristata* Pursh, *Heliathella uniflora* (Nuttall) Torrey and Gray, *Helianthus nuttallii* (Torrey and Gray, *Verbesina* (as *Actinomeris*) sp., *Wyethia helenioides* (deCandolle) Nuttall, and *Xanthium strumarium* L. (as *enceliodes*) (Wasbauer, 1972). *Balsamorhiza*, *Encelia*, *Helianthus*, *Heliathella*, *Geraea*, *Verbesina*, *Viguiera*, and *Wyethia* all are members of the subtribe

Table 1. Examples of synphagy among *Neotephritis finalis* and *Trupanea* sp. in flower head samples from native Asteraceae in southern California.

Host Plant	Replicate	Number (%) of Tephritidae Reared	
		<i>N. finalis</i>	<i>Trupanea</i> spp.
<i>Encelia californica</i>	1	30 (19.0)	<i>T. wheeleri</i> 128 (81.0)
	2	12 (18.7)	<i>T. wheeleri</i> 52 (81.3)
	3	20 (9.1)	<i>T. wheeleri</i> 199 (90.5)
			<i>T. nigricornis</i> 1 (0.5)
<i>E. farinosa</i>	1	1 (3.2)	<i>T. nigricornis</i> 30 (96.8)
	2	30 (46.9)	<i>T. nigricornis</i> 34 (53.1)
<i>E. frutescens</i>	1	14 (45.2)	<i>T. nigricornis</i> 17 (54.8)
	2	14 (87.5)	<i>T. nigricornis</i> 2 (12.5)
<i>E. virginensis</i>	1	10 (66.7)	<i>T. wheeleri</i> 4 (26.6)
	2	1 (1.5)	<i>T. nigricornis</i> 1 (6.7)
			<i>T. nigricornis</i> 64 (98.5)
			<i>T. nigricornis</i> 166 (99.4)
<i>Geraea canescens</i>	1	73 (92.4)	<i>T. jonesi</i> 4 (5.1)
	2	7 (46.7)	<i>T. bisetosa</i> 2 (2.5)
			<i>T. bisetosa</i> 7 (46.7)
			<i>T. jonesi</i> 1 (6.6)
	3	23 (95.8)	<i>T. jonesi</i> 1 (4.2)
	4	11 (73.3)	<i>T. bisetosa</i> 4 (26.7)

Verbesininae of the tribe Heliantheae, and thus form a natural assemblage of host plants (Munz and Keck, 1959). Unconfirmed host records from the genera *Dahlia* and *Xanthium*, which belong to other subtribes of Heliantheae, are somewhat less suspect than records from *Aster* in the tribe Astereae or *Eriophyllum* and *Gaillardia* in the tribe Helenieae (Munz and Keck, 1959; Bailey, 1975). However, Hilgendorf and Goeden (1983) never reared *N. finalis* from flower heads or otherwise collected this fly from *X. spinosum* L. or *X. strumarium* during extensive faunistic surveys of these weeds in southern California.

Synphagy.—Cavender (1981) reported that *N. finalis* was the third most common species of Tephritidae in the flower heads of cultivated and wild sunflower, *H. annuus*, in southern California after *Paracantha cultar*is (Coquillett) and *Trupanea bisetosa* (Coquillett). During 1980–86, RDG consistently reared *N. finalis* together with one or two species of *Trupanea* from samples of

flower heads of four species of *Encelia* and *Geraea canescens* (Table 1). These samples were collected from different locations, usually in different years. *Trupanea bisetosa*, *T. jonesi* Curran, *T. nigricornis* (Coquillett), and *T. wheeleri* Curran variously were associated with *N. finalis* in these flower heads (Goeden, 1985). The same two or three species usually emerged from flower heads of each plant species; however, none of the four *Trupanea* species was recovered from all samples (Table 1), nor was *N. finalis* always recovered (Goeden, unpublished data). The proportions of these synphagous tephritid species varied among samples and hosts, with *N. finalis* acting either as the dominant, middle level, or subordinate species, sometimes in different samples from the same species of host plant (Table 1). This interpretation assumes that the numbers of flies of each species reared from each sample reflect the results of interspecific competition for their common flower-head resources. Synphagy is a common form of

resource sharing among flower head-infesting Tephritidae in southern California (Goeden, unpublished data). Indeed, synphagy apparently is a characteristic life history strategy for certain genera, e.g. Nearctic *Urophora* (Goeden, 1987).

BIOLOGY

The biology of *N. finalis* was studied in the field and insectary by TDC largely in and near the Botanic Garden of the University of California, Riverside, during 1982 and 1983 on one of its most common and widespread native hosts in southern California, *Encelia farinosa* (Table 1). As the flower heads of this host, as well as cultivated and wild sunflowers, commonly contained *Trupanea nigricornis* and *Melanagromyza viridis* (Frost) (Diptera: Agromyzidae), the studies of Cavender (1981), published in part as Cavender and Goeden (1982, 1983), helped TDC distinguish *N. finalis* during the present study. Immature flower heads protected from oviposition by small plastic bags in the field for up to 4 days were uncovered and offered to caged females in the insectary of the Division of Biological Control, during studies of fecundity, longevity, and behavior during courtship, mating and grooming. Insectary conditions were $27 \pm 2^\circ\text{C}$, 40–60% RH, and 16-h photoperiod. Cages used were described by Gilstrap and Goeden (1974).

Egg.—The egg is smooth, translucent white, elongate ellipsoidal, blunt posteriorly, but tapered anteriorly. Fifty eggs measured 1.15 ± 0.10 ($\bar{x} \pm \text{SEM}$) (range, 1.09–1.24) mm long by 0.27 ± 0.02 (range, 0.23–0.31) mm wide. The egg was laid singly between the florets with its posterior end touching the pappus above its juncture with the achene. In the insectary, 116 (98.3%) of 118 eggs hatched in 2 days; the remaining two eggs, in 3 days.

Larva.—Before hatching, the embryo took about 10 min. to reverse its position inside the egg, then fed for about an hour on a gel-like substance inside the posterior end be-

fore exiting through a posterior slit-like break in the chorion. Upon hatching, the larva immediately entered the immature achene and began to feed. After eating through the achene, the larva moved laterally into an adjacent achene and continued to tunnel in this fashion through a succession of disc achenes throughout its growth and development. Dissection of field-collected flower heads of *E. farinosa* indicated that first instars perforated 3 to 6 achenes, second instars tunneled through an additional 3 to 9 achenes, and third instars attacked another 7 to 11 achenes, of which the contents of 3 to 5 were completely consumed. When larvae fed on sunflower achenes, the first stadium lasted about 2 days (range, 2–4; $N = 118$); the second stadium, about 3 days (range, 2–6; $N = 114$); and the third stadium, about 7 days (range, 4–14; $N = 82$).

Pupa.—Pupariation occurred at the terminus of the larval mine in a cell made of frass, slightly larger than the puparium. The puparium is oblong, slightly tapering anteriorly, translucent light brown to medium brown, with very distinctive, dark brown remnants of the anterior and posterior spiracles. Thirty δ puparia averaged 3.5 ± 0.2 (range, 3.1–3.9) mm in length by 1.5 ± 0.1 (range, 1.2–1.6) mm in greatest width. Twenty f puparia averaged 3.7 ± 0.1 (range, 3.4–3.9) mm long by 1.6 ± 0.1 (range, 1.4–1.6) mm wide. The puparium rested atop the receptacle, usually with its anterior end from which the adult emerges facing outward, separated from the outside by a thin layer of frass. Fifty-three adults emerged from their puparia an average of 9 (range, 6–14) days after pupariation under insectary conditions.

Adult.—Mating was not observed in nature. In insectary cagings, mating behavior was initiated as a male approached a female while flexing his wings alternately. One wing was thrust forward perpendicular to the long axis of the body, while the other wing was held outward at about 15° . The wings then alternated in these positions at about 1 s

intervals, while the male moved forward at about 2 mm per s. Meanwhile, the female mainly stood still, but also alternately flexed her wings in response. When the pair faced each other about 7 mm apart, the male brought both wings backward at 15°, as the female reversed her position and faced away. The male then flexed both wings forward together and quickly mounted her posteriorly. Coupling followed in about 4 s, after the female lifted her ovipositor, into which the male inserted his aedeagus. Coupling lasted until the female disengaged herself from the generally passive male. Nine pairs were observed in *copula* an average of 6 (range, 2–11) times, for an average of nearly 3 h (range, 36 min.–7.5 h) for 30 individual matings timed from start to finish in the insectary. The nonreceptive or just-mated female dislodged the male by brushing him off with her hindlegs, by moving her ovipositor downward and away from the male, or by folding her wings over her abdomen as a barrier to copulation.

Fighting was observed in the field and insectary. This involved males that faced each other about 7 mm apart and alternately flexed their wings forward. The defender then suddenly rushed forward and butted the intruder with his head. Females similarly employed forward thrusts of their bodies, sometimes accompanied by synchronized forward thrusts of their wings, to confront and ward off intruders, including ants that usually ignored these actions. Generally, however, individual flies exhibited nonaggressive behavior and spent considerable time resting or grooming themselves. In the insectary, 45- to 60-day-old females were continuously quiescent for 3 to 5 h, except for the normal pumping motion of their mouthparts. In the field and the insectary, males were motionless for as long as 2 h. Both sexes groomed their wings with their hindlegs; the head, eyes, and antennae were groomed with the front legs. The characteristic rubbing of both front or hindlegs after grooming apparently removed debris.

Adults occasionally exhibited a swaying movement in the field and insectary, whereupon the body was rocked from side to side. This behavior usually was exhibited during the approach of a moving object, and possibly helped the fly to distinguish an intruder or potential mate. During preparation for flight, both sexes assumed a characteristic posture with the head lifted, the long axis of the bodies slanted upward, and the front and middle legs extended outward.

Oviposition and ovipositor probing was observed in the field from 7 AM to 5 PM on spring days; however, these activities peaked during mid-day. These were the most common activities of fecund females on flower heads in the field. Instances of males attempting to mate with ovipositing females were observed, but these nonreceptive females fended off the males with thrusts of their heads, flew away, or behaved as described above to prevent mating.

The ovipositing female walked upon a flower head while examining it, occasionally stopping to probe the florets with her ovipositor. Upon locating a suitable site, she bent her ovipositor downward and inserted it between the florets, the tip reaching the precise location previously described. Deposition of each egg took about 20 to 60 s, after which searching behavior resumed. Sometimes a female would interrupt her search to walk down the pedicel for a short distance then return to the head and continue her examination. Dissections of 20 *E. farinosa* flower heads in which females had recently oviposited yielded an average of 3 (range, 1–5) eggs.

Twenty pairs (each 1 ♂ and 1 ♀) produced an average of 37 (range, 11 to 141) eggs in insectary cagings. Individual females laid an average of 19 (range, 1–36) eggs per day on days when eggs were laid. The mean ovipositional period was 21 (range, 16–30) days, the mean age at last oviposition was 41 (range, 26–56) days, and the mean ovipositional period was 16 (range, 1–54) days.

Seasonal history.—*Neotephritis finalis* is multivoltine in southern California. Adults have been collected throughout the year, with reproduction occurring in low desert areas in winter, e.g. on *Helianthus niveus*, and continuing in a succession of low and high desert, interior valley, and coastal, host-plant species in blossom in spring along a gradient of increasing altitude and rainfall, e.g. on *Geraea* and *Encelia*. In summer, this reproduction by *N. finalis* continues in hosts in mountain areas, e.g. *Balsamorhiza* and *Wyethia*. In the fall, this reproductive activity and, probably, adult migration, again moves downward and continues in hosts such as fall-blooming species of *Helianthus*.

Natural enemies.—*Eurytoma vernonia* Bugbee (Erytomidae) and *Pteromalus* sp. (Pteromalidae), which are primary, solitary, larval or larval-pupal parasites, were reared from flower heads of *Encelia farinosa*. Both species were confirmed as parasites of *N. finalis* and probably also parasitize *Trupanea nigricornis* and, perhaps, *Melanagromyza viridis* in these heads.

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LITERATURE CITED

- Bailey, L. H. 1951. Manual of Cultivated Plants. MacMillan Pub. Co., Inc., New York, 1116 pp.
- Cavender, G. L. 1981. Life Histories of *Trupanea bisetosa* (Coquillett) and *Paracantha cultaris* (Coquillett) on *Helianthus annuus* L. (Compositae) in Southern California, with Notes on *Trupanea nigricornis* (Coquillett) (Diptera: Tephritidae). M.S. Thesis, Univ. Calif., Riverside, 187 pp.
- Cavender, G. L. and R. D. Goeden. 1982. Life history of *Trupanea bisetosa* (Diptera: Tephritidae) on wild sunflower in southern California. Ann. Entomol. Soc. Am. 75: 400-406.
- . 1983. On distinguishing *Trupanea bisetosa* (Coquillett) from *T. nigricornis* (Coquillett) (Diptera: Tephritidae). Proc. Entomol. Soc. Wash. 85: 275-281.
- Coquillett, D. W. 1902. New acalypterate Diptera from North America. J. N.Y. Entomol. Soc. 10: 177-191.
- Foote, R. H. 1960. The species of the genus *Neotephritis* Hendel in America north of Mexico (Diptera, Tephritidae). J. N.Y. Entomol. Soc. 68: 145-151.
- Foote, R. H. and F. L. Blanc. 1963. The fruit flies or Tephritidae of California. Bull. Calif. Insect Surv. 7, 115 pp.
- Gilstrap, F. E. and R. D. Goeden. 1974. Biology of *Tarachidia candefacta*, a Nearctic noctuid introduced into the U.S.S.R. for ragweed control. Ann. Entomol. Soc. Am. 67: 265-270.
- Goeden, R. D. 1985. Host-plant relations of *Trupanea* spp. (Diptera: Tephritidae) in southern California. Proc. Entomol. Soc. Wash. 87: 564-571.
- . 1987. Host-plant relations of native *Urophora* spp. (Diptera: Tephritidae) in southern California. Proc. Entomol. Soc. Wash. 89: 269-274.
- Hilgendorf, J. H. and R. D. Goeden. 1983. Phytophagous insect faunas of spiny clotbur, *Xanthium spinosum*, and cocklebur, *Xanthium strumarium*, in southern California. Environ. Entomol. 12: 404-411.
- Loew, H. 1862. Diptera Americae septentrionalis indigena. Centuria secunda. Berlin. Entomol. Ztschr. 6: 185-232.
- Munz, P. A. 1974. A Flora of Southern California. Univ. Calif. Press, Berkeley and Los Angeles, 1086 pp.
- Munz, P. A. and D. D. Keck. 1959. A California Flora. Univ. Calif. Press, Berkeley and Los Angeles, 1681 pp.
- Steyskal, G. C. 1972. A preliminary key to the species of *Neotephritis* Hendel (Diptera: Tephritidae). Proc. Entomol. Soc. Wash. 74: 414-416.
- Wasbauer, M. W. 1972. An annotated host catalog of the fruit flies of America north of Mexico (Diptera: Tephritidae). Calif. Dep. Agric. Bur. Entomol. Occas. Pap. 19, 172 pp.